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THE REPRODUCTIVE STRUCTURES OF FRAXINUS
VELUTINA (OLEACEAE)

HERBERT F. COPELAND

The observations on floral structure and embryogeny in *Fraxinus velutina* Torrey, called the Arizona ash, which are here presented, were undertaken because an abundance of material was available; and because the facts as to Oleaceae assembled in Schnarf's (1931) *Vergleichende Embryologie der Angiospermen* were fragmentary, including no reasonably complete account of any single species.

Material was collected from trees cultivated on the grounds of Sacramento City College during the years 1957 to 1959. It was treated by routine microtechnical methods: fixed in Bouin's fluid and stained with Delafield's haematoxylin, Heidenhain's haematoxylin, or safranin and light green.

In the library, consulted when a certain acquaintance with the plant had been attained, I found out that the microscopic reproductive features of the Oleaceae are no longer poorly known; also, that there has been disagreement as to the proper place of Oleaceae in the taxonomic system. These matters are discussed in later sections of this paper.

THE TREE

Fraxinus velutina occurs near springs and along streams in western Texas, New Mexico, Arizona, and southern California. Pratt (1922?) wrote of it as apparently new in cultivation and recommended it as resistant to alkali and drought. It is widely planted in northern California, where it is seen to survive with little or no irrigation, but to flourish in watered lawns.

Munz and Lauder milk (1949) refer all plants of this species which are native in California to var. *coriacea* (Watson) Rehder, and I have been uncertain of the identity of the cultivated material. Taylor (1945) found the species diploid ($2n = 46$) and the variety tetraploid ($2n = 92$). The cultivated trees are diploid ($n = 23$), and are to be referred to the species.

As a typical ash, this is a deciduous tree bearing opposite pinnate leaves and producing samaras. It belongs to the group of ashes in which the flowers are apetalous and dioecious. Flower clusters appear in the axils of the proximal fallen leaves of the previous year during the month of February. Pollination is evidently by wind. In March, the staminate flowers fall, and the leaves begin to unfold. The samaras grow to their full size by the end of May, but the seeds are not mature until autumn. The samaras are shed, along with the leaves, in autumn storms.

The flower clusters are dense glomerules. After anthesis, the axes of the pistillate clusters become elongate, and it is seen that they are freely branched in a decussate pattern. All of the flowers or fruits of a particular

cluster are at a particular time in nearly the same stage of development; most axes bear terminal flowers; hence, the clusters are to be construed as thyrses.

MALE STRUCTURES

The staminate flower (fig. 1) consists, beyond its receptacle, of a calyx which is reduced to a minute toothed cup and of two stamens having brief filaments and prominent basifixed extrorse anthers. The vascular supply of this flower (fig. 2) consists of a cylinder of tissue originating from the two sides of a bract gap, emitting a cycle of a small indefinite number of feebly developed traces to the calyx, and then splitting into two bundles which ascend the connectives of the anthers to their summits.

The anthers are of the structure usual in flowering plants. The cells of the endothecium duly develop ribbed walls, and the dehiscence of the anthers, which occurs through the usual two lengthwise clefts, is produced by their contraction. The tapetum is of the secretion type. The nuclei of the tapetal cells divide more than once, and then undergo fusions, with the result that just before the tapetum is absorbed its cells contain varying numbers of large nuclei with varying numbers of nucleoli (figs. 3, 4).

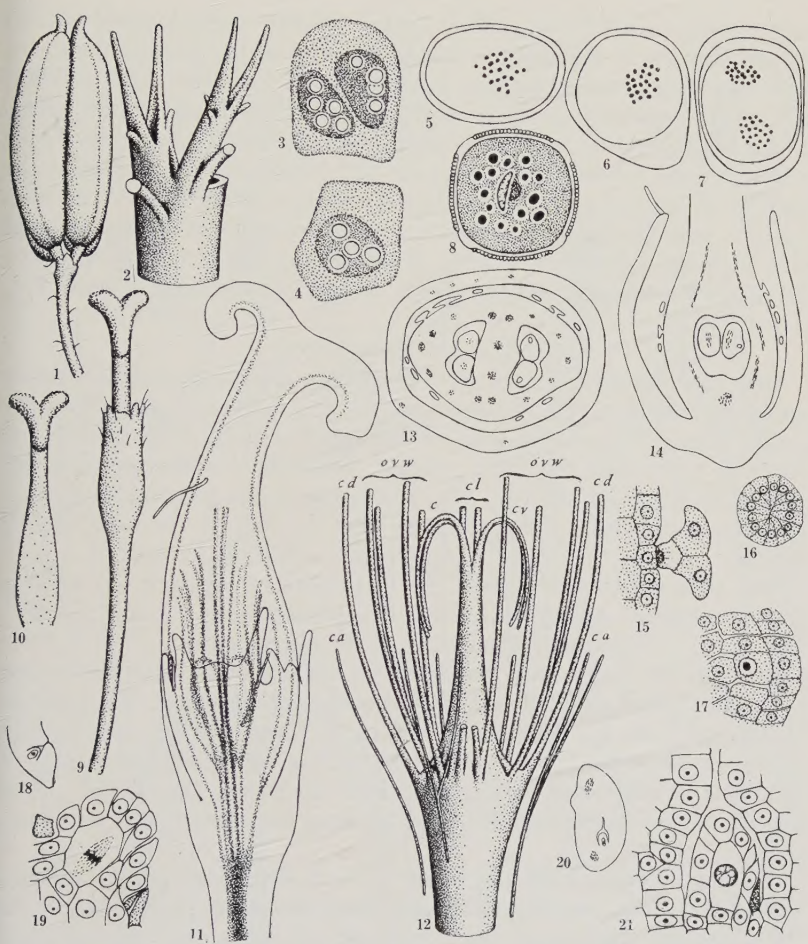
The haploid chromosome number, observed during meiosis in the pollen mother cells, is 23 (figs. 5, 6, 7). The pollen grains are separated by simultaneous furrowing. When mature, they are four-grooved, having the surfaces between the grooves finely pitted, and contain a tube nucleus and a generative cell (fig. 8).

THE PISTILLATE FLOWER

The pistillate flower (fig. 9) consists, beyond its receptacle, of a cup-shaped calyx with a dentate margin and a compound pistil of two carpels. The ovary contains two locules. The septum between the locules is punctured by a small cleft near its upper end: the upper ends of the locules are continuous. Each locule contains two ovules which are pendant from the distal area of the septum. The ovary is flattened contrary to the narrow septum (fig. 13); the flattening is moderate through most of the height of the ovary, but is greater in the upper part. The brief style is cylindrical. The stigma is of two lobes which are pressed together when the flowers are first exposed but become separate at anthesis. The stigmatic surface is papillose.

The ovary bears a moderate number of peltate trichomes (figs. 15, 16) which are of the same nature as those which occur on leaves of *Syringa* and *Ligustrum*. The pedicel and flower bear also a few simple hairs, mostly on the margin of the calyx.

The vascular system supplying this flower is as follows (figs. 11, 12). The usual cylinder of vascular tissue ascends the pedicel. The calyx contains a whorl of a varying number of feebly developed bundles which fade out below. This means that the stele in the pedicel supplies only the pistil. The stele gives rise to an outer whorl of about fourteen bundles including (a) two well-marked carpel-dorsals, respectively ascending the



FIGS. 1-21. *Fraxinus velutina*: 1, staminate flower $\times 8$; 2, vascular supply of two staminate flowers, $\times 40$; 3, 4, mature cells of the tapetum, $\times 720$; 5, 6, pollen mother cells with nucleus in heterotypic metaphase, $\times 720$; 7, pollen mother cell with nucleus in heterotypic anaphase, $\times 720$; 8, pollen grain, $\times 720$; 9, pistillate flower, $\times 8$; 10, pistil, $\times 8$; 11, pistillate flower cleared in chlorine water, $\times 20$; 12, model of vascular system in lower part of the pistillate flower, $\times 40$; 13, cross section of young ovary, $\times 40$; 14, longitudinal section of young ovary, $\times 40$; 15, 16, radial section and surface view of scale of ovary, $\times 320$; 17, archesporial cell of young ovule, $\times 320$; 18, 19, longitudinal section of developing ovule, $\times 40$, and nucellus of same showing megaspore mother nucleus in heterotypic metaphase, $\times 320$; 20, 21, longitudinal section of ovule, $\times 40$, and nucellus of same showing megaspore mother cell, $\times 320$. *ca*, sepal bundles; *cd*, carpel dorsal bundles; *cl*, carpel lateral bundles; *cv*, carpel ventral bundles; *ovw*, ovary wall bundles.

margins of the ovary and continuing up the style into the stigmatic lobes; (b) a total of about eight ovary wall bundles, being about two on each

side of each carpel dorsal; and (c) a pair of well-marked carpel-laterals at each margin of the septum. Above the level of the locules, the ovary wall bundles and carpel laterals spread apart to form two fan-like layers toward the respective surfaces of the flattened upper part of the ovary. These bundles do not enter the style, but fade out. The vascular tissue which ascends beyond the departure of the whorl just described takes the form of an attenuate cone ascending the septum of the ovary. The cone splits to form two bundles located toward the margins of the septum, and each of these, toward the summit of the septum, splits in turn into two bundles which diverge and turn down to supply two ovules lying in different locules.

OVULE AND EMBRYO SAC

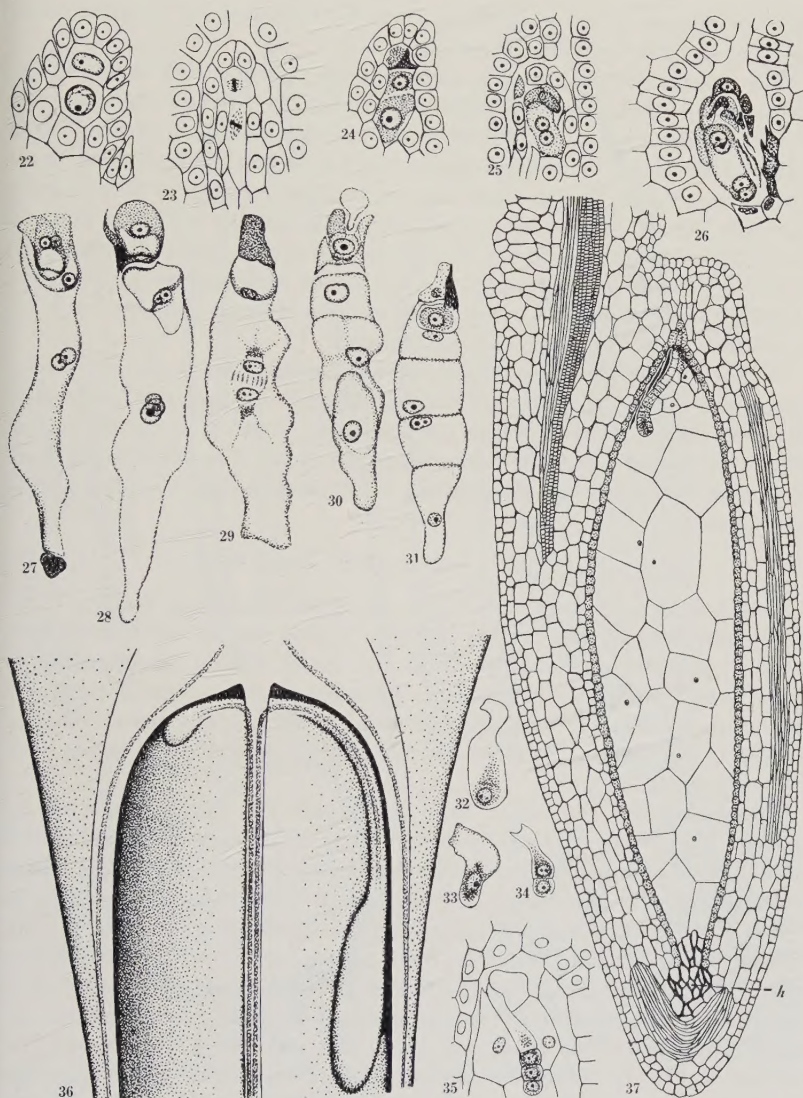
When the pistillate flowers are first exposed, before the stigmatic lobes swing apart and become receptive, one finds in each locule two immature ovules (figs. 13, 14) of the form of downward-pointing fingers. Each one contains a strand of immature vascular tissue. Each contains one hypodermal archesporial cell (fig. 17). The archesporial cells are located on the sides of the ovules which are away from the plane of the carpel-dorsal bundles: one sees them best in sections cut parallel to the septum.

The archesporial cell is itself the megaspore mother cell. It becomes elongate, and the epidermis covering it is pushed up as a scanty nucellus (figs. 19, 21). The tissue on all sides of the nucellus grows forth to form an integument. The growth is greatest on the side of the nucellus toward the original tip of the ovule, which now becomes the chalaza. The effect of this growth is to turn the nucellus toward the summit of the ovary, and to enclose it except for a narrow micropyle leading up from it (the growth of the ovule is illustrated only by two little diagrams, figs. 18, 20). The mature ovule is somewhat flattened between the septum and the ovary wall.

During the growth of the ovule as just described, spiral tracheids appear in the main bundle which runs down the raphe to the chalaza. At the same time, several additional bundles begin to undergo differentiation in the integument. These latter bundles, few but not of definite number, usually three or four, extend the length of the ovule from the end of the original bundle, in the chalaza, nearly to the level of the micropyle.

While the integument is growing up about the nucellus (fig. 18), the meiotic divisions of the nucleus of the megaspore mother cell, and the accompanying cell divisions, begin to take place (figs. 19, 22-24). A T-shaped tetrad of megaspores is produced. The spore at the chalazal end is functional.

The nucleus of the functional megaspore undergoes three successive divisions, while the three non-functional spores and the nucellus are absorbed (figs. 25, 26; the stage with eight free nuclei has not been seen). An embryo sac with an egg and two synergids, two polar nuclei and three antipodal cells, is organized (fig. 27). The antipodal cells appear moribund from the time when they are set apart, and soon disappear. During



FIGS. 22-37. *Fraxinus velutina*: 22, nucellus showing diad cells, $\times 320$; 23, homeotypic metaphase, $\times 320$; 24, tetrad of megaspores, $\times 320$; 25, 2-nucleate embryo sac, $\times 320$; 26, 4-nucleate embryo sac, $\times 320$; 27, mature embryo sac, $\times 320$; 28, fertilization, $\times 320$; 29, first division of endosperm nucleus, $\times 320$; 30, 31, zygote and endosperm in 4-celled stage, $\times 320$; 32, 33, zygote about one month after fertilization, $\times 320$; 34, first division of zygote, $\times 320$; 35, four-celled embryo in many-celled endosperm, $\times 320$; 36, dissection of lower part of fruit about two months after fertilization, $\times 20$; 37, longitudinal section of seed at same stage as in fig. 36, $\times 80$. *h*, hypostase.

the development of the embryo sac, the inner epidermis of the integument takes on the character of a jacket layer.

The meiotic divisions appear always to take place earlier in one of the four ovules of the ovary than in the others (figs. 18, 19 show the beginning of meiosis before the integument is fully developed; figs. 20, 21 show a fully formed ovule in which meiosis has not begun). Through all later stages, one ovule is always found in a more advanced stage of development than the others. More ovules than one may develop complete embryo sacs; pollen tubes may enter more than one ovule; but only the ovule which developed most rapidly is capable of maintaining an embryo. Developed embryo sacs in other ovules undergo degeneration by a process of collapse which begins at the chalazal end.

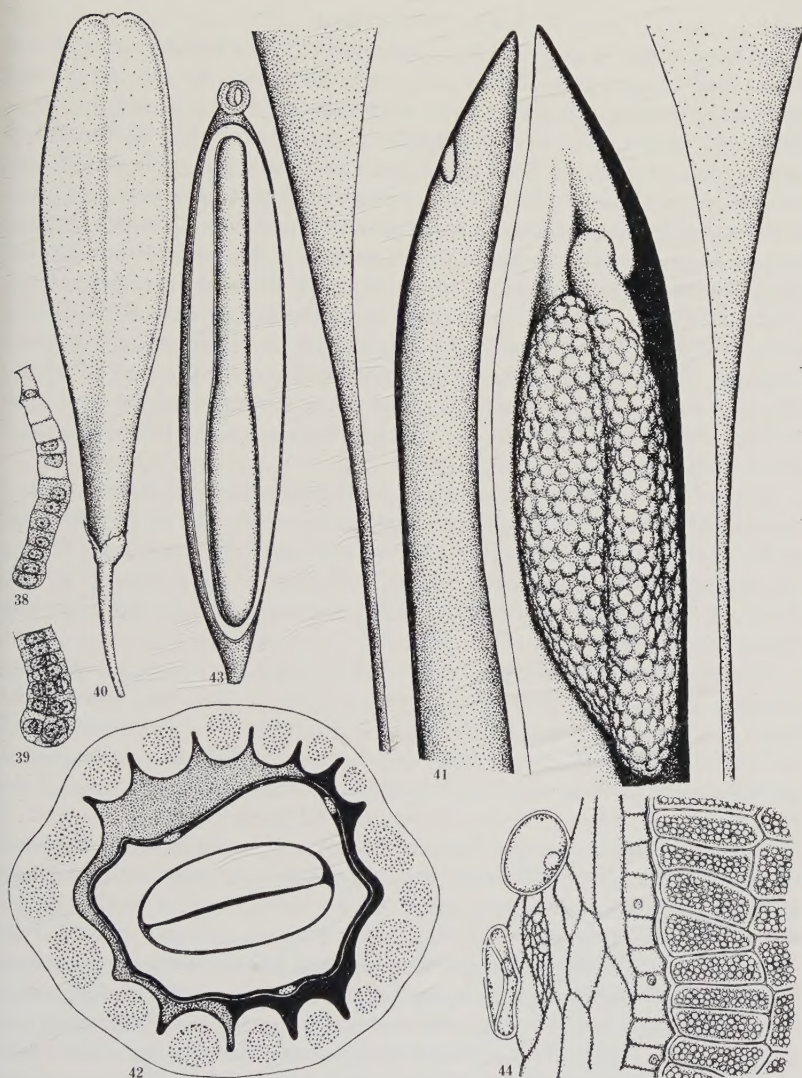
When the embryo sac is ready for fertilization, the ovule contains a hypostase, consisting of a small body of differentiated chalazal cells. It is recognizable by cell walls which are relatively retentive of the dye safranin; in sections stained with haematoxylin alone, it is not recognizable. It is separated from the chalazal end of the embryo sac by a few undifferentiated cells.

FERTILIZATION, ENDOSPERM, AND EMBRYO

Pollen tubes have been seen in the micropyles of various ovules. Their discharged tips, of the form of heavily staining masses, have been seen between pairs of synergids in which the nuclei remain recognizable: it appears that both synergids survive for some time after the entrance of the pollen tube. On several slides, one sperm nucleus has been seen near the egg nucleus, while the other sperm nucleus is in process of fusing with the polar nuclei (fig. 28).

The endosperm is cellular from its origin. The first division of its nucleus (fig. 29) is followed by deposition of a transverse wall. The divisions of its daughter nuclei are followed by the deposition of walls which are transverse or nearly so: the endosperm passes through a stage in which it is a linear (or nearly linear) tetrad of cells (figs. 30, 31). During further multiplication, the cells of the endosperm do not become differentiated except for the crushing of some of them at the micropylar end; no haustoria are produced. The chalazal end of the endosperm digests or crushes the cells of the chalaza as far as the hypostase. For the rest, the endosperm does not digest the adjacent cells. It appears to press upon the jacket layer and the hypostase, and the integument grows along with the endosperm.

Fertilization having taken place early in March, the zygote remains undivided until about the beginning of May, by which time the endosperm is already many-celled. Before the zygote divides, it may become enlarged (figs. 32, 33). After it divides, the enlargement disappears; there is no exceptionally swollen cell at the base of the suspensor (figs. 34, 35). Dividing transversely, the zygote and its progeny produce a uniseriate filament of a dozen or more cells (figs. 37-39). The definitive embryo



FIGS. 38-44. *Fraxinus velutina*: 38, 39, embryos from same collection as figs. 36 and 37, $\times 320$; 40, mature fruit, $\times 4$; 41, dissection of lower part of mature fruit, $\times 20$; 42, cross section of lower part of mature fruit, $\times 20$; 43, dissection of seed (much longer than the one in fig. 41), $\times 8$; 44, section of outer part of seed, seed coat to the left and endosperm to the right, $\times 320$.

originates by longitudinal divisions in several cells at the distal end of this filament. The proximal cells lose their stainable contents, shrink, and disappear.

FRUIT AND SEED

Between early March and late May, growth of the ovary produces a samara of mature size. There are great differences in rate of growth between different parts of the ovary and different dimensions of the parts. The lower part of the ovary, originally a small moderately flattened cylinder, retains this shape while growing to seven or eight times its original dimensions. The upper part, while undergoing slight increase in thickness, grows to some fifteen times its original width and fifty times its original length. Thus it produces the wing of the samara. The wing is not derived from the style, which persists, if at all, as a withered terminal scrap.

The internal septum of the ovary, originally a wall with nearly plane surfaces, undergoes swelling immediately after fertilization and becomes fusiform. The bundles of the ovary wall become greatly enlarged by the differentiation of masses of fibers and form vertical ribs on the inner surface. Septum and ribs fill the locules, leaving scant clefts of complicated form.

Of the four ovules which are hung from the upper part of the septum, three undergo no growth, but turn dark and shrivel. The fourth develops at its proximal end a long funiculus which holds the main body of the developing seed at about the middle of the height of the septum (fig. 36). During the growth of the funiculus, its surface is thrown into microscopic transverse ridges.

The seed proper, enlarging principally after the beginning of July, reaches dimensions approximately half of those of the lower part of the fruit, that is, of the fruit apart from the wing (fig. 41). In the course of this growth, the seed presses into, and largely crushes, the enlarged septum. It pushes back the funiculus, throwing it into coils. The surface of the mature seed is yellow to brown, shiny, and minutely papillate.

Dissection shows the seed to have a thin coat covering an endosperm in which lies a large cylindrical embryo divided through the distal half of its length into two cotyledons (figs. 42, 43). The papillae on the surface of the seed are enlarged epidermal cells. The jacket layer, that is, the internal epidermis of the integument, remains intact. With the exception of the papillae, the jacket layer, and small bodies of fibers in the four or five longitudinal bundles, the cells of the integument are compressed and nearly empty. A definite continuous wall at the outer margin of the endosperm belongs to the endosperm, not to the jacket layer. The cells of the endosperm are packed with granules (fig. 44). These are definitely not of starch; they appear to be of protein.

DISCUSSION

Schnarf's account of the embryology of Oleaceae consisted of scattered observations upon *Forsythia*, *Jasminum*, *Ligustrum*, and *Fraxinus* in the classic general papers of Hofmeister (1858), Warming (1878), Guignard (1882), Billings (1901), Juel (1915), and Dahlgren (1923, 1927). Sommer (1929) had studied *Fraxinus excelsior* among various plants in which

a distinction among the ovules of a single ovary, some continuing their development and others undergoing abortion, appears suddenly at a certain stage of development. Eames (1931) included *Syringa* and *Forsythia* among plants in which he studied the vascular supply of the pistil. Subsequent embryological studies include those of Andersson (1931) on a wide variety of Oleaceae, and of King (1938) and Messeri (1950) on the domestic olive, *Olea europaea*. Johnson (1941) included *Forsythia* among plants in which he studied the cytology of the male gametophyte. Fotidar (1942) studied the floral anatomy of *Nyctanthes*. Numerous counts of chromosomes are reported by Sax (1930), O'Mara (1930), Sax and Abbe (1932), Taylor (1945), and Dutt (1952); the contribution of Taylor is particularly interesting as including counts for *Fraxinus velutina* and its varieties, and as proposing to limit the subfamily Oleoideae to genera in which the basic chromosome number is 23, thus excluding *Jasminum* and *Menodora*.

The observations on *Fraxinus velutina* here presented are in very nearly complete agreement with the facts as to Oleaceae in general as stated in the literature just cited. Andersson noted in various Oleaceae the peculiar tapetum, characteristic of widely scattered presumably derived groups, in which the nuclei divide more than once. Johnson found the pollen grains of *Forsythia* binucleate. The vascular supply of the pistil, alike in *Syringa*, *Ligustrum*, *Nyctanthes*, and *Fraxinus*, exhibits slight variations upon a common pattern which is precisely that of the typical bicarpellate compound pistil according to the theory of Eames. The pattern of the vascular supply to the ovules is identical in *Olea* and *Fraxinus*. Billings was presumably mistaken in describing, in the ovule of *Fraxinus excelsior*, a single vascular strand which descends the raphe to the chalaza and ascends the integument on the side opposite the raphe. In *F. velutina*, as noted, a varying small number of bundles, in positions which vary from one ovule to another, run up from the chalaza; Fotidar observed the same structure in *Nyctanthes*. Also, as Dahlgren suspected, Billings was surely mistaken in figuring an ovule in which the megaspore mother cell is covered by more than one layer of cells of the nucellus: this appearance represents an oblique section of the ovule. In most Oleaceae, the embryo sac is of normal type and the definitive embryo develops from several distal cells of a filamentous early embryo. In these points, *Olea* appears exceptional: its embryo sac is said to be of *Scilla*-type and its filamentous early embryo is very short.

The proper location of Oleaceae in the taxonomic system is next to be discussed. The traditional place of the family is in an order named Contortae. The order was established by Linnaeus (1764) to include the plants subsequently assembled as families Apocynaceae and Asclepiadaceae. Of *Olea* and its allies, Linnaeus made a separate order Sepiariae; he placed *Gentiana* among primulaceous plants in his order Rotaceae. Eichler (1886) and Engler (1892) are responsible for assembling as order Contortae the families Oleaceae, Loganiaceae, Gentianaceae,

Apocynaceae, and Asclepiadaceae. In earlier presentations of the Englerian system, one finds the small tropical family Salvadoraceae placed next to Oleaceae; in later presentations it is dismissed from this neighborhood, surely correctly, since the ovules of Salvadoraceae have two integuments and a nucellus of more than one layer of cells (David, 1938). Wettstein (1908) followed Linnaeus and most pre-Englerian authors in placing Oleaceae in an order (he called it Ligustales) separate from Contortae. Schnarf followed Wettstein, although expressing doubt that the families remaining in Contortae belong together as a natural group. Wettstein (1908) is authority for family Menyanthaceae, a segregate from Gentianaceae, and Schnarf (1931) is authority for family Buddleiaceae, a segregate from Loganiaceae. Tournay and Lawalrée (1952) transferred Menyanthaceae and Buddleiaceae from Contortae to Ligustales.

Schnarf, and Tournay and Lawalrée, were influenced by embryological knowledge, including particularly the following point. The endosperm is nuclear in proper Loganiaceae and Gentianaceae, and in Apocynaceae and Asclepiadaceae. It is cellular in Buddleiaceae, Menyanthaceae, and Oleaceae.

Assuming that the production of a nuclear endosperm is a primitive character from which the production of the cellular endosperm has repeatedly been derived, the presence of both types in a particular order or family is not by itself sufficient reason for dividing the group. We can interpret Loganiaceae, Gentianaceae, Apocynaceae, and Asclepiadaceae as a natural series in which the primitive type of endosperm is retained, and Buddleiaceae and Menyanthaceae as offshoots from it in which the derived type of endosperm has developed independently. This appears to be the idea of Moore (1947), who considers Loganiaceae to be an immediate ally or derivative of some primitive stock from which have evolved also the Tubiflorae (among which a repeated evolution of the cellular endosperm is evident) and the Rubiales (which retain the nuclear endosperm).

The Buddleiaceae have a cellular endosperm with haustoria (Moore describes these as absent in *Polyprenum*, but one of his figures shows structures to which no other term can be applied) and an embryo developed from two cells terminal upon a three-celled suspensor (Souèges, 1940; Moore, 1948).

Of Menyanthaceae, the writer has learned nothing beyond what was known to Schnarf. A tapetum in which the nuclei divide more than once; an embryo sac of normal type, with fugitive antipodal cells; a cellular endosperm in which cell divisions beyond the first are transverse, and which lacks haustoria; and an early embryo of the form of a many-celled filament: all of these are characters in precise agreement with Oleaceae. To present knowledge it appears probable that the Oleaceae are derived from the Menyanthaceae and should be placed after that group.

SUMMARY

1. *Fraxinus velutina* Torrey, the Arizona ash, a tree of the southwest-

ern United States, is a typical ash of the group having dioecious apetalous flowers. The flowers and their vascular systems are described. The vascular system of the pistillate flower is very nearly that of the typical bicarpellate compound pistil according to the theory of Eames.

2. Staminate flowers consist of little more than two stamens with ribbed endothecia and tapeta in which the nuclei divide more than once and then undergo random fusions. The haploid chromosome number is 23. Pollen grains are 4-grooved, binucleate.

3. The ovules are unitegmous and tenuinucellate. They have several longitudinal bundles in the integument and an obscure hypostase in the chalaza. The inner epidermis of the integument becomes a jacket layer. Of four ovules in the ovary, only one becomes a seed.

4. The embryo sac is of normal type, the antipodal cells disappearing quickly.

5. Double fertilization was observed.

6. The endosperm is of cellular type. The first cell division is by a transverse wall; the second cell divisions are by walls which are transverse or nearly so. No haustoria are produced.

7. The zygote, after remaining undivided for several weeks, produces a filament of many cells. The embryo proper is derived from several cells at the distal end of this filament.

8. The single seed of the samara crowds aside or crushes other structures within the ovary and becomes mature in autumn. Papillae upon its surface are enlarged epidermal cells. The jacket layer persists to this stage. A continuous wall within the jacket layer is the outer cell wall of the endosperm. There is a large straight dicotyledonous embryo.

9. These observations, compared with others in the literature, tend to substantiate the naturalness of the family Oleaceae and the order Contortae. Among other Contortae, the Menyanthoideae appear most similar to Oleaceae in embryological characters.

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A NEW SILENE FROM NORTHWESTERN CALIFORNIA

A. R. KRUCKEBERG¹

Long past is the era in California botany when a collector could count among his season's haul a good proportion of undescribed species. Most areas of the state are sufficiently well known so as to limit the likelihood of uncovering anything new. Nowadays, range extensions, records of new adventures, and the discovery of some inconspicuous annual that fails to

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match any known relative, serve to satisfy the field botanist's taste for novelties. When a hitherto undescribed perennial which is an element of a stable plant community is found, it is of more than passing interest. Such discovery is most likely in the relatively little explored mountainous terrain of northwestern California. *Silene marmorensis* Kruckeberg, described below, is one of these latter day discoveries, having been collected in 1954 by Dr. C. Leo Hitchcock along the forested slopes of the Marble Mountains in southwestern Siskiyou County.

For the past eight years, I have been maintaining a collection of living plants of North American species of *Silene*. The plants have been grown for purposes of observation under uniform conditions, for determining chromosome number (Kruckeberg 1953, 1960), and for assessing degree of genetic relationships by means of interspecific hybridization (Kruckeberg 1954). The genus is represented in California by twenty native species (*sensu* Hitchcock and Maguire 1947), nearly all of which are well represented in herbaria. Moreover, most of them are readily distinguishable and thus stand out as clearly defined species. Having worked with living plants of all the Californian species as well as most of the known species occurring elsewhere in North America, I was genuinely impressed with a specimen that did not fall into place with any known species.

In general habit, *Silene marmorensis* might be confused with the Sierra Nevada *S. verecunda* Wats. subsp. *platyota* (Wats.) H. & M., both having long, flexuous stems and short, lanceolate leaves. In inflorescence and floral characters, though, the new species combines features of at least three species—*S. campanulata* Wats., *S. lemmonii* Wats., and *S. bridgesii* Rohrb.—all of which share, as well, the common characteristics of an ovoid, cartilaginous capsule and large black seeds; in addition, all four species are tetraploid ($2n = 48$). The new species appears most closely related to *S. bridgesii* of the yellow pine belt in the Sierra Nevada, owing to the close correspondence of the two species in inflorescence and flowers. However, in *S. marmorensis*, the flowers are not pendant, nor do the proportions of its calyx, petals, and style match those of *S. bridgesii*.

The suite of characters which defines *S. marmorensis* can be summarized as follows. The several wiry, weakly ascending stems bear 5–7 pairs of uniformly short, lanceolate leaves; the open, lax, glandular inflorescence bears 4–6 pairs of lateral cymules, with the cymules consisting of single flowers in wild plants and the lateral flowers apparently abortive; the flowering calyces are elongate, ovate-lanceolate, and are borne divaricately on thin, wiry pedicels. The pinkish petals have a simple, bifid blade at the base of which are the two laterally divaricate, erose auricles; the appendages are short and rather broad. No one of these features is specific for a western *Silene*, but in ensemble, they contrive to give a picture of a rather delicate, unassuming grace and uniqueness to the plant (figs. 1–3).

Having examined only two collections of *S. marmorensis*, it would be rash to attempt a delimitation of its distribution and habitat preference.

The two specimens cited below were collected along the steep, winding forest road leading northeast up to Camp Three from the confluence of the Salmon and Klamath rivers at Somes Bar. The terrain is steep, forested mountainside with a south to southwest exposure. A topotype collection (*Kruckeberg 4023*) grew in loose talus of gabbroic rock in a fairly open stand of Douglas fir, black oak, and madrone. A list of associated species is appended to the species description.

Silene marmorensis sp. nov.² Planta perennis tenui radice; caudice caulibus compluribus tenuibus, 2.5–4.0 dm. longis, puberulentis, supra glandulosis; foliis caulinis 5–7 paribus, fere eadem magnitudine, lanceolatis, 3.0–4.5 cm. longis, 0.3–0.5 cm. latis, scabrido-pubescentibus; bracteis reductis, lineari-lanceolatis, glandulosis; inflorescentibus terminalibus, 10–20 cm. longis, fere simplicibus, cymulis 5–7 iugis, pedicellis 7–10 mm. longis, filiformibus, glandulosis; calyce 13 mm. longo, anguste elongato-ovato, glanduloso, minus valide 10-nervo, lobis late lanceolatis, 3 mm. longis; calyce in fructu campanulato; corolla supra ex rubro pallea, infra subviridilurido (galbino), ungue 8–10 mm. longo, glabrato, sursum latiore, auriculo parvo eroso in utroque summae latere, lamina 4–6 mm. longa oblongata, alte bilobata, lobis integris vel in apice tenuiter erosis, appendicibus 2, oblongatis; staminibus exsertis, in tubo compressis, filamentis 11–13 mm. longis, glabratis, polline subfusco; stipitibus 3–4 mm. longis, puberulentis; stylis 3, 10–12 mm. longis, filiformibus, papillis stigmatum paucis et tantummodo in apice styli; ovariis glabratis ovatis maturitate et ligno-cartilagineis et 5-dentatis; seminibus 2.5 mm. longis, nigris, fulgentibus, tuberculis ex ordinibus brevibus conicis.

Perennial, from a long slender taproot, the multicapital crown bearing several underground, erect branches, each of which terminates above ground in a slender stem, 2.5–4.0 dm. long, stems simple, purplish and eglandular-pubescent at base, retrorsely glandular-pubescent above, especially on branches of inflorescence; the 5–7 pairs of cauline leaves similar in size and shape, reduced only in the inflorescence, lanceolate, 3.0–4.5 cm. long, 0.3–0.5 cm. wide, sparsely scabrid-pubescent on both surfaces, the leaf-like bracts of inflorescence progressively reduced upwards, short-lanceolate, glandular; inflorescence terminal, 10–20 cm. long, simple, or with 1–2 branches, each bearing 5–7 pairs of cymules (the lateral flowers of each cymule apparently abortive in field material); pedicels 7–10 mm. long, filiform, glandular; calyx in flower indistinctly 10-nerved, glandular, narrowly elongate-ovate, slightly constricted at base, about 13 mm. long, becoming campanulate through distension by the maturing ovary, the teeth ovate-lanceolate, short-acuminate, 3 mm. long, somewhat membranous in the sinuses, margins of teeth densely long-ciliate; corolla pale pink above, greenish yellow beneath, the claw 8–10 mm. long, glabrous throughout, slender at base widening above, with a small erose, angular auricle at either side of summit, the blade 4–6 mm. long, oblong, bilobed

² The Latin diagnosis kindly prepared by W. M. Read, Professor of Classics, University of Washington.



FIG. 1. Type specimen of *Silene marmorensis*, Hitchcock 20221 (WTU 179156), $\times \frac{1}{3}$.

over one-half its length, the lobes oblong, entire to slightly erose at tip, appendages two, broadly oblong, truncate, the free margins entire; stamens slightly exserted, crowded at throat, the filaments 11–13 mm. long, glabrous throughout; pollen tawny brown in color; carpophore 3–4

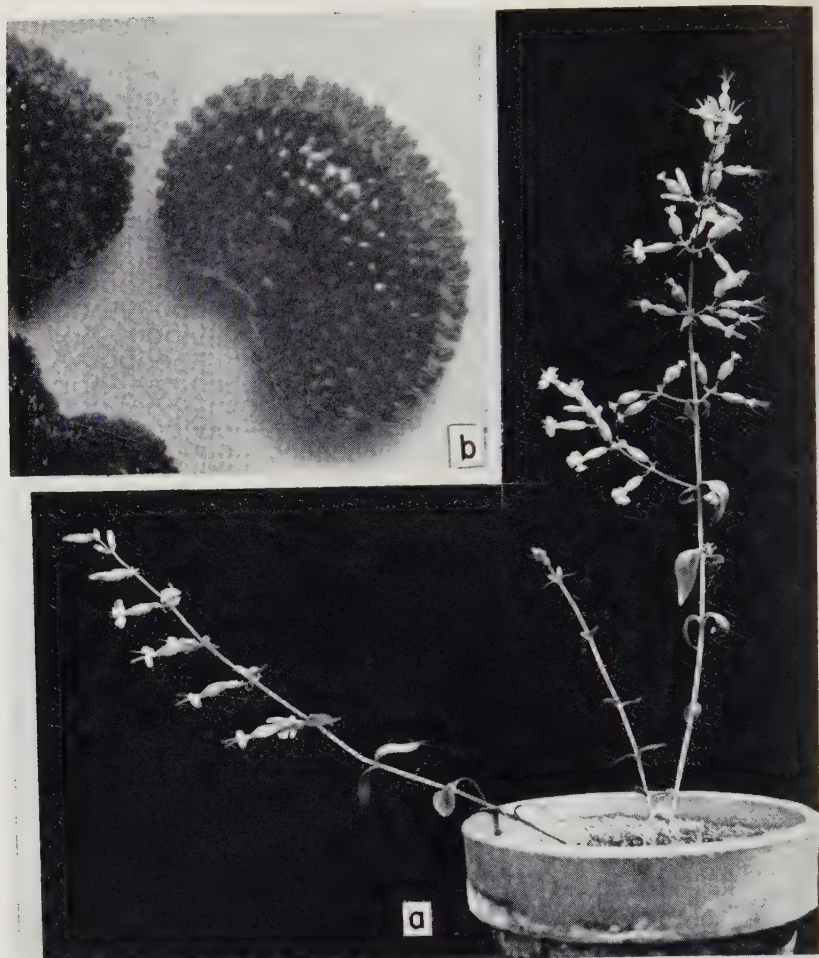


FIG. 2. *Silene marmorensis*: a, plant grown in greenhouse (photo by W. Martin, Still Photo Unit, University of Washington); b, seed, \times ca. 20.

mm. long, retrorsely puberulent; styles three, 10–12 mm. long, filiform, nearly straight, the stigmatic papillae few and congested at tip; ovary glabrous, at maturity ovoid with walls woody-cartilaginous, opening with five teeth; seeds about 2.5 mm. long, black, shiny, with concentrically longitudinal rows of short conical tubercles. $2n = 48$. Figs. 1–3.

Type. Siskiyou County, California: 1.0 mile north of Somes Bar on road to Camp Three, June 22, 1954, *C. L. Hitchcock* 20221 (WTU 179156); another specimen (topotype) from 5.5 miles above Somes Bar on road to Camp Three, growing in loose talus of gabbroic rock, *A. R. Kruckeberg* 4023 (WTU 172672). Some of the vegetation associated with *Kruckeberg* 4023 is as follows: *Pseudotsuga menziesii*, *Quercus*

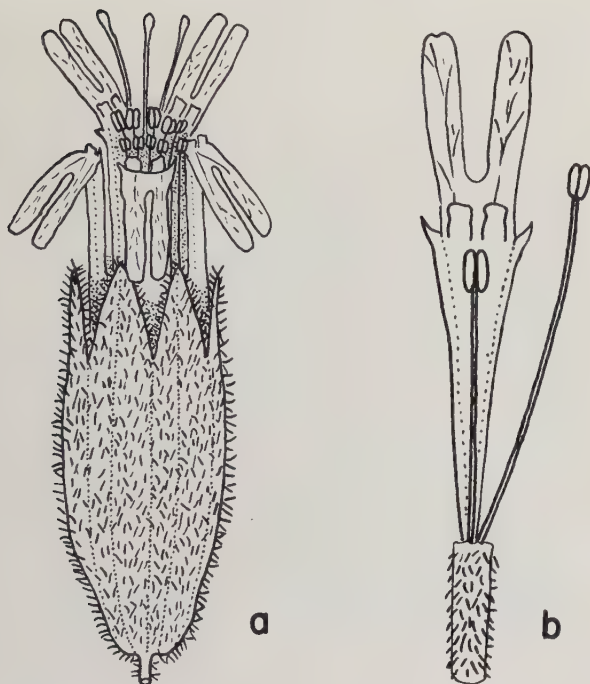


FIG. 3. Flower of *Silene marmorensis*: a, single whole flower; b, carpophore with attached single petal and stamen. All $\times 7$.

kelloggii, *Arbutus menziesii*, *Cornus nuttallii*, *Quercus chrysolepis*, *Acer macrophyllum*, *Pinus lambertiana*, *P. ponderosa*, *Lithocarpus densiflora*, *Corylus californica*, *Ceanothus integerrimus*, and *Cercis occidentalis*; also a sparse covering of such herbaceous plants as *Cynoglossum occidentale*, *Poa* sp., *Galium* sp., *Stephanomeria* sp., *Polystichum lemmonii*, *P. munitum*, *Pteridium aquilinum*, *Hieracium albiflorum*, *Eriophyllum lanatum*, *Iris* sp., and *Smilacina racemosa*.

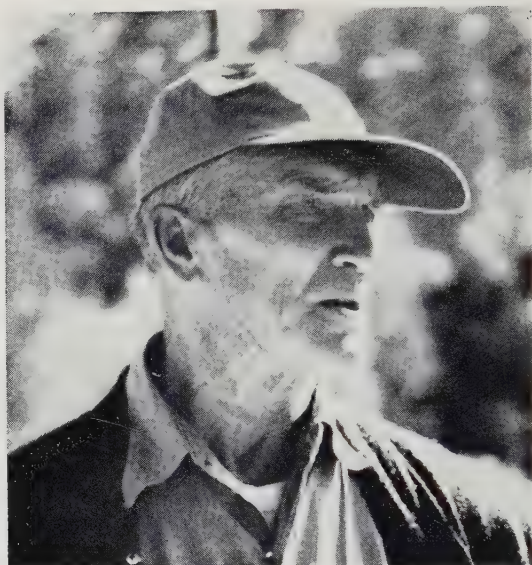
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FREED HOFFMAN

1880-1959



The botanical career of Mr. Freedom W. Hoffman, who died at his home near Guerneville, California, 13 November 1959, spanned a fifty-year period. Freed was born at Knights Landing, Yolo County, 30 January 1880, where he lived until he went away to school at about the age of fifteen. As his mother was of French descent, Freed learned, as a child, to speak French and he retained his fluency and interest in this language throughout his life. Following his graduation from Chico Normal School he studied art in New York City for several years. Upon his return to California he began a teaching career in which he achieved considerable success for something over a decade.

On 24 August 1907, Freed married Jemella Gertrude Peugh. Throughout the forty-seven years of their married life, Jimmy regularly accompanied Freed on trips into the remote back country. In the early days such trips were made with burro or mule, while later a Jeep served a similar purpose.

While at Berkeley soon after his marriage, Freed became principal of the LeConte School, to which he often referred in later years as the first Junior High School in America. At about this time Freed studied with Professor Setchell and Professor Gardner in the Botany Department at the University of California at Berkeley. He mentioned to me several times Dr. Gardner's offer of a teaching assistantship which, while it tempted him, was rejected in favor of a teaching position at San Francisco Normal School.

I first met Freed and Jimmy at their home near Guerneville in the early summer of 1941. Freed had sent some interesting specimens of *Streptanthus* to the Herbarium at the University of California, Berkeley, for identification. In order to meet the collector and see the populations of plants, I drove to Guerneville. From the beginning of our eighteen-year friendship I was charmed by Freed. His slow, patient, deliberate approach to problems made a real impression on me.

Because I was interested in *Streptanthus* and its distribution in relation to serpentine soils, because I enjoyed being with Freed and Jimmy, and because I could collect abundant fresh flowering plant material near Guerneville for class use, I went back to the Hoffmans' several times during the summer of 1941. On one occasion Freed and I spent several days beginning the construction of a cabin on a remote hunting claim, which Freed had proven to be still part of the public domain in 1910 and 1911 even though it had previously changed hands several times in land deals. Careful search of land office records and many weekends spent surveying had finally enabled him to file on the quarter section as a hunting claim. Its chief value lay in the existence of a spring not far below a ridge top. Freed and I hunted deer, fruitlessly, in the early mornings and the early evenings. During the day we began a cabin to replace the old one built by Freed in 1911. As we leisurely cut and notched the sill logs, Freed recounted, interspersed with discussions of the Pythagorean theorem, his reasons for leaving teaching to become an orchardist.

Freed Hoffman was a man with a very considerable artistic talent. His oils and watercolors with which their home and guest cottage were hung made a lasting impression on all who saw them. The intricate woodcarving on the massive lauan loom which he built for Jimmy was still another evidence of his creative ability. As a carpenter, stone mason, botanist, botanical artist, Freed's accomplishments were of professional quality. Certainly his abilities as a teacher were equally great. Yet he resigned his teaching position, left a career for which he seemed well fitted, and still in his thirties, took over the management of the extensive orchards owned by himself and Jimmy near Guerneville.

With brush and palette, with hammer and saw, with pruning hook and picking basket and ultimately with plant press and seed bed, Freed found that he could see and sense the results of his labors almost immediately, while in teaching often many years passed before results were evident. Freed had the kind of patient sensitivity that would lead him to cut down his fruit picking speed by half in order not to discourage completely a youngster during his first day on the ladder, but he simply could not wait the many years to be greeted by a former pupil, now a mature man, who might say, "You probably don't remember me, Professor Hoffman, but you taught me geometry. . . ."

With the realization in 1941 that serpentine outcroppings often supported unusual populations of plants, Freed began a series of botanical trips which eventually brought his collections over the 4000 mark. Among

his collections from remote and little-known serpentine areas is the type specimen of *Haplopappus ophitidis* (J. T. Howell) Keck. An *Allium* collected by Freed is likely to be the type of a new species. Especially in the genus *Streptanthus*, in which he published two new species in 1952, Freed's numerous collections have increased greatly our knowledge of variation and geographic distribution.

When World War II ended and gasoline, as well as new vehicles, became readily available, Freed purchased a Jeep in which he and Jimmy traveled widely in search of serpentine and "Streps." Jimmy's death in June, 1953, following their return from an extensive collecting trip in the Southwest, was a blow from which Freed found it almost impossible to recover. A trip to the Piedmont of North Carolina to visit Jimmy's relatives and the thoughtful solicitude of friends finally restored in Freed his former interests.

On 7 April 1955 Freed married Blanche Lenora Greden, who survives him. Blanche's lively interest in Freed's botanical studies and her devoted care during the trying time of Freed's stroke and his lengthy and arduous convalescence have endeared her to those of us who came to know her through Freed.

Freed's ties with the profession of botany were primarily with members of the California Botanical Society and the personnel of the Herbarium at Berkeley. He corresponded rather regularly with Bacigalupi, Carter, Kruckeberg, McMillan, Mason, Morrison, and others interested in serpentine, *Streptanthus*, or both. His collections, his watercolor sketches, especially of *Streptanthus*, and his voluminous notes on various sections of this genus are on deposit in the Herbarium of the University of California at Berkeley.—JOHN L. MORRISON, State University, College of Forestry, Syracuse University.

CLEARED CARDIOCARPON LATE-ALATUM LESQ., CORDAITEAN SEEDS FROM MICHIGAN¹

J. F. DAVIDSON

Arnold (1948) described *Spermatites cylix* from the Big Chief No. 8 mine at St. Charles, Michigan, as appearing to be the apical portion of a very large spore. The present account may throw some light upon the nature of the object so designated, while extending our knowledge of the material previously identified (Arnold, 1949) as *Cardiocarpon late-alatum* Lesq.

The Cordaitean seed that Lesquereux described as *Cardiocarpon late-alatum* (1879, Pl. LXXXV, figs. 46, 47; 1880, p. 568) is a small, rounded, slightly cordate body, about 9 mm. wide and 10 mm. long. The nucule,

¹ This work was financed in part by a grant from the University of Nebraska Research Council.

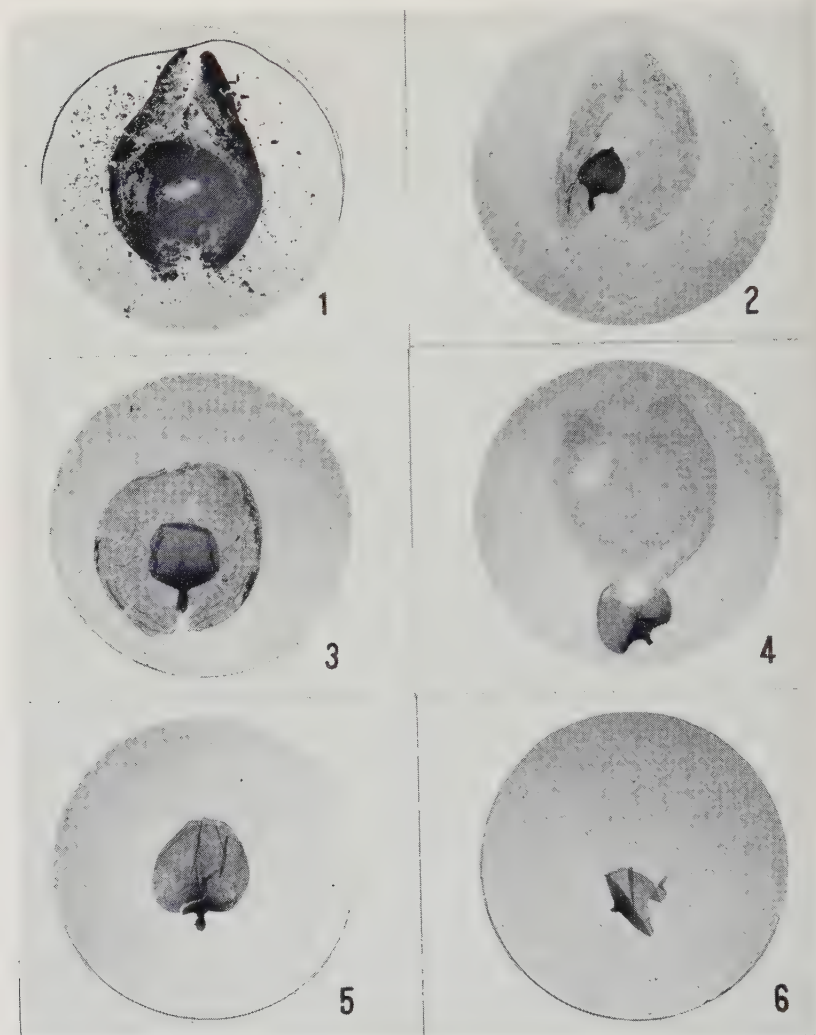
as figured, is about 5 mm. wide, and is surrounded by a marginal wing which varies from 2 to 3 mm. in width. The apical portion of the wing is only slightly prolonged. Lesquereux expressed uncertainty about the validity of the distinction between this species and *C. zonulatus* and *C. simplex*, all three being from the sub-conglomerate at Pittston, by saying: "Perhaps these three forms, separated as species, represent the same, although the differences appear evident" (1880, p. 569). Of these three species, however, the specimens from Grand Ledge, Michigan, which are discussed below, show the closest resemblance to Lesquereux' figures 46 and 47 which represent *C. late-alatum*. While Lesquereux was familiar with Brongniart's work in which the name *Cardiocarpon* was used for silicified seeds, he based his own separations on characters expressed in compressions.

In 1955, large numbers of *Cardiocarpon* seeds were collected at Grand Ledge, Michigan. These occurred in the shale immediately below what Kelly (1933) designated as "Cycle A" in his Pennsylvania stratigraphy. In the dried shale, the seeds could be studied only as compressions, but when freshly-collected shale was submerged in water the shale immediately started to disintegrate and some of the seeds, as well as other plant remains, could be recovered.

An attempt to clear the seeds with concentrated nitric acid and potassium chlorate (Schultz's solution) and 1 per cent ammonium hydroxide resulted in quite opaque preparations (fig. 1). This was apparently due to the intrusion of shale within the layers of the integument, and was eliminated by soaking the seeds in hydrofluoric acid previous to clearing. Such seeds were dehydrated in alcohol before mounting permanently in Diaphane.

In addition to the more or less complete seeds, several other isolated fragments were cleared. Some of these fragments were portions of the nucellar region of the seed, which showed no evidence of the previously-surrounding integument tissue. During the clearing and mounting process, the nucellar portions showed a strong tendency to become separated from their enveloping integuments. Since the cuticle of the integument is more delicate than that of the nucellus, it is logical that the latter would be occasionally preserved after the disintegration of the surrounding integument.

With the variation evident in these seeds, together with the variation originally recognized by Lesquereux, we are faced with two alternatives as regards the disposition of the specimens within our nomenclatural system. If we accept the names proposed by Lesquereux as denoting three species of Paleozoic seeds, then we can validly apply his names only to those specimens which agree exactly with his figured and described types. This implies that the vast majority of specimens which do not so agree will have to be described as new species. This might well be the case here. The alternative deals with probabilities. Since Lesquereux stated that his specimens from the same habitat were *possibly* conspecific, and since



FIGS. 1-6. *Cardiocarpon late-alatum* Lesq. (Circles are 18 mm. in diameter.) FIG. 1. Mature seed. (Without treatment with hydrofluoric acid, the intruded shale obscures detail. Other figures are cleared after treatment with hydrofluoric acid. Figures 2-5 show gradually increasing size of nucellus). FIG. 2. Nucellus, although displaced in clearing, shows apical beak. FIG. 3. Nucellus in position. FIG. 4. Displaced nucellus, showing heavily cutinized basal region. FIG. 5. Nucellus found free in the shale. The integument was not preserved. FIG. 6. Portion of the base of a nucellus, found free. (This is the kind of structure described as *Spermatites cylix* Arnold, the type of which was studied in comparison.)

comparable material has been found in another single habitat at Grand Ledge, it is *probable* that the variations encountered represent slight differences in the preservation process, and differences in the ages of the seeds when shed. The latter point is illustrated in the figures, which show variation not only in the over-all size of the seeds, but also in the size of the nucellar region. Were abortion involved, one might reasonably expect to find a series of small, aborted seeds and another series of more or less mature seeds, without the intermediate sizes.

Of the foregoing alternatives, the latter appears the more logical, and less apt to result in a confusion of names. In the material collected at Grand Ledge, some of which is figured here, it is assumed that the variation encountered represents differences in the maturity of individual seeds, and differential preservation of conspecific material. Thus it is here all referred to *Cardiocarpon late-alatum* Lesq.

The seeds from Grand Ledge are flattened, circular to ovate in outline, 9–15 mm. long by 9–11 mm. broad. The basal region shows an indentation at the point of attachment, which extends almost to the swollen basal stalk of the nucellus, while the distal end appears as a deeply bifid beak. The surface of the integument appears to be composed of roughly isodiametric cells, approximately 45 microns in diameter, except for those of the wing, which are about 20–25 microns broad and 60–100 microns long. The wing starts as a narrow band about 0.5 mm. wide near the base of the seed, and gradually increases in width upward to an observed maximum of 2.0 mm. In these specimens, the integuments, with the exception of the wings, were filled with clay, apparently bound with silica, since hydrofluoric acid dispersed it.

The nucellar body is very heavily cutinized, ovoid to globose, 2–7 mm. long, and equally broad. At the proximal end, a compact tissue of heavily-walled cells forms a saucer-shaped base (figs. 4, 5) which in turn arises from a short, 1 mm. long cylinder of similar cells in which no vascular tissue is apparent. The base of this cylindrical stalk is somewhat swollen, the cell walls are thinner, the cells are slightly larger and have a glandular appearance. The tendency for the nucellar portion to separate from the integument is shown in figures 2 and 4, while figure 5 shows the heavily cutinized base of the nucellus beginning to break away from the upper portion, in a specimen found without the surrounding integument. In figure 5 also may be seen the region of attachment of the nucellar stalk to the integument. Figure 6, which is one of the fragments found in the shale and cleared, is merely the basal portion of the nucellar region of a seed.

Although the apex of the nucellar body appears to be rounded in most specimens, closer examination shows that the specimens are incomplete. The smallest (fig. 2) and the largest (fig. 1) individuals show a definite attenuation at the apex such as might be expected to lead to a pollen chamber.

The specimen shown in figure 6 was compared with the type material

of *Spermatites cylix* Arnold, and they appear to be conspecific. Hence, *Spermatites cylix* probably refers to the basal portion of a nucellus from a Cordaitan seed comparable to *Cardiocarpon late-alatum*.

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THE BASIC CHROMOSOME NUMBER OF THE GENUS NEPTUNIA

(LEGUMINOSAE-MIMOSOIDEAE)

B. L. TURNER AND O. S. FEARING

The genus *Neptunia* is composed of about ten or eleven species of annual and perennial herbs. Its members are widely distributed in the tropical and subtropical regions of the world. Five species are endemic to the Old World (three in Australia, two in India); two are cosmopolitan, occurring in wet habitats, principally in tropical regions; and three or four are confined to North and South America.

The region with the greatest number and diversity of taxa appears to be Texas and adjacent Mexico where four or five species are represented (Turner, 1951). From a standpoint of floral morphology, this area also retains one of the least modified species in the genus (*Neptunia lutea*)¹.

The first chromosome count reported for a species of the genus was by Dnyansagar (1952). He reported a number of $n = 18$ from sectioned anther material of the Indian species, *N. triquetra*. However, the camera lucida drawing documenting this count appears to show 18 somatic chromosomes and is perhaps but a portion of the complement of a single somatic cell of premeiotic "mother cell" tissue.

Turner and Beaman (1953) reported counts for three unnamed American taxa of *Neptunia* as $2n = 28$. Their counts were obtained from somatic cells of sectioned root tip material. The only other report for the genus has been that of Frahm-Leliveld (1953) who listed an approximate

¹ All of the described taxa in the genus, except this species, have some flowers with anantherous staminodia modified into petaloid structures. *N. lutea* has flowers with the stamens all alike and anther-bearing.

TABLE 1. SPECIES OF NEPTUNIA EXAMINED FOR CHROMOSOME NUMBER

Species	Seed Source and Voucher Collection	Chromosome Number
* <i>Neptunia dimorphantha</i> Domin	AUSTRALIA (Seed communicated by Div. of Plant Industry, C.S.I.R.O., Canberra City). <i>Q227</i>	$2n = 28$ (fig. 3)
* <i>Neptunia gracilis</i> Benth.	AUSTRALIA (As above) <i>C884</i>	$2n = 56$
* <i>Neptunia monosperma</i> Benth.	AUSTRALIA (As above) <i>W652</i>	$2n = 28$ (fig. 2)
<i>Neptunia plena</i> (L.) Benth.	INDONESIA (Reported by Frahm-Leliveld, 1957)	$2n = 78?$
<i>Neptunia triquetra</i> Benth.	INDIA (Reported by Dnyansagar, 1952).	$n = 18?$
* <i>Neptunia prostrata</i> (Lam.) Baill.	INDIA. Raipur (Seed communicated by Dr. V. R. Dnyansagar). <i>Turner s.n.</i>	$2n = 56$ (fig. 1)
* <i>Neptunia lutea</i> (Leavenw.) Benth.	TEXAS. Galveston County: <i>Turner 2189</i>	$2n = 28$ fig. 5)
* <i>Neptunia lutea</i> (Leavenw.) Benth.	TEXAS. Galveston County: <i>Turner 2923</i>	$2n = 28$
* <i>Neptunia pubescens</i> var. <i>floridana</i> (Small) Turner	TEXAS. Galveston County: <i>Turner 2194</i>	$2n = 28$
* <i>Neptunia pubescens</i> var. <i>lindheimeri</i> (B. L. Robinson) Turner	TEXAS. San Patricio County: <i>M. C. Johnston 541338</i>	$2n = 28$ (fig. 4)

* Indicates new report for the genus.

count for *N. plena* as $2n = \pm 72$; in a later paper Frahm-Leliveld (1956) in reporting the same species, apparently settled on the number $2n = 78$, though the drawing documenting this count is not easily interpreted.

Because of the differing base numbers for the genus reported by these workers, and because of the known unibasic nature of most genera in the Leguminosae, the present authors have reinvestigated the previous reports for the taxa reported by Turner and Beaman and in addition have investigated four species previously unreported.²

MATERIALS AND METHODS. Chromosome counts listed as new in the present paper (Table 1) were made from root tip cells of germinating seeds using a squash technique outlined by Turner and Fearing (1959). Polyploid cells were noted in the tissue of all the taxa examined, though diploid cells appeared to be more common and this is the number given in Table 1.

RESULTS AND DISCUSSION. Altogether, counts for eight of the approximately ten species in the genus have been reported (Table 1). Except for the doubtful count of $n = 18$ for *N. triquetra* and the count of *N. plena*

² Attempts to obtain seed of the controversial *N. triquetra* have been unsuccessful. The authors are grateful to Dr. V. R. Dnyansagar who so kindly furnished the seed of *N. prostrata* used in the present study.



FIGS. 1-5. Camera lucida drawings of the mitotic chromosomes in *Neptunia* spp.: 1, *N. prostrata* ($2n = 56$); 2, *N. monosperma* ($2n = 28$), late metaphase, 2 pair of chromosomes have already separated and are shown in the "unpaired" condition; 3, *N. dimorphantha* ($2n = 28$); 4, *N. pubescens* var. *lindheimeri* ($2n = 28$), prophase; 5, *N. lutea* ($2n = 28$). (\times ca. 1200.)

($2n = 78$), all reported counts have been on a base of $x = 14$. The species here reported are from taxa occurring on several continents, and one of them, *N. lutea*, has a "primitive" floral structure and occurs in a region where several diverse taxa are found. These facts make a base number of $x = 14$ for the genus seem more plausible than that of a multibasic pattern, particularly since *N. triquetra* and *N. plena* are not especially different morphologically from species with known counts of $2n = 28$. In addition it might be noted that related genera of the tribe Adenanthereae, in which *Neptunia* is usually included, are also on a base of $x = 14$ (e.g. *Prosopis* and *Dichrostachys*, Darlington and Wylie, 1956).

SUMMARY

Chromosome numbers for six species of *Neptunia*, all on a base of $x = 14$, are presented for the first time. These counts were obtained from diverse species which occur naturally in Australia, India and Texas. In view of the known constancy of base numbers for most genera of the Leguminosae, and in view of the poor documentation for differing base

numbers reported by other workers, it has been concluded that $x = 14$ is probably the correct base chromosome number for the genus.

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HYBRIDIZATION AND INSTABILITY OF YUCCA

JOHN MILTON WEBBER¹

The contention that hybridization is largely responsible for the widespread variability of southwestern yuccas (2,4,9)² is supported by the following facts. 1) Cross-pollination is enhanced by the yucca's dependence upon the yucca moth for pollination. 2) Two or more species frequently occur in mixed stands or near each other. 3) The karyotypes of all species are strikingly similar (cf. 1). 4) Inter- and intra-specific pollinations produce equally abundant seed. 5) There is little difference in the degree of relationship and the ability to hybridize. 6) Many variants exhibit specific characteristics of two or more species. 7) Apparent hybrids are frequently more fertile than "typical" species. 8) Progenies of apparent hybrids are composed of two or more types. These facts, however, pertain only to putative hybrids and the conditions favoring hybridization. Although a few garden and artificial hybrids (3,8) have been cited, their characteristics, behavior, and fertility have not been recorded. The present study of artificial hybrids indicates that yuccas are genetically similar and that hybridization among native plants is common.

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² Numbers in parentheses refer to Literature Cited.

The seeds of the species involved in the hybrids were collected in the following localities:

Yucca glauca Nutt., Grant, New Mexico.

Yucca elata Engelm., White Sands National Monument, New Mexico.

Yucca constricta Buckl., Big Spring, Texas.

Yucca schidigera Roezl ex Ortgies, Riverside, California.

Yucca arizonica McKelv., Nogales, Arizona.

Yucca neomexicana Woot. & Standl., Kenton, Oklahoma.

The pollinations were made at Riverside, California (9), and the hybrids were grown in the University of California Botanic Garden, Berkeley, California. Specimens of the hybrids are in the University of California Herbarium, Berkeley, California.

FERTILITY AND MEIOTIC BEHAVIOR

The percent of F_1 fruit obtained from self-pollinations and the viability of F_1 and F_2 seed are given in Table 1.

The microsporocyte divisions of the hybrids were identical or strikingly similar. Each consistently formed 5 large and 25 small bivalents and exhibited few or no irregularities in either the first or the second division. All tetrads appeared normal, and only 6 percent of the matured grains were abortive.

TABLE 1. PERCENT OF F_1 SELFED FRUIT AND VIABILITY OF F_1 AND F_2 SEED

	Percent germination of F_1 seed*	Percent of F_1 fruit from self-pollinations*	Percent germination of F_2 seed
<i>Y. glauca</i> \times <i>Y. elata</i>	84	88	86
<i>Y. constricta</i> \times <i>Y. schidigera</i>	64	72	72
<i>Y. arizonica</i> \times <i>Y. neomexicana</i>	54	24	68
<i>Y. arizonica</i> \times <i>Y. glauca</i>	62	32	72

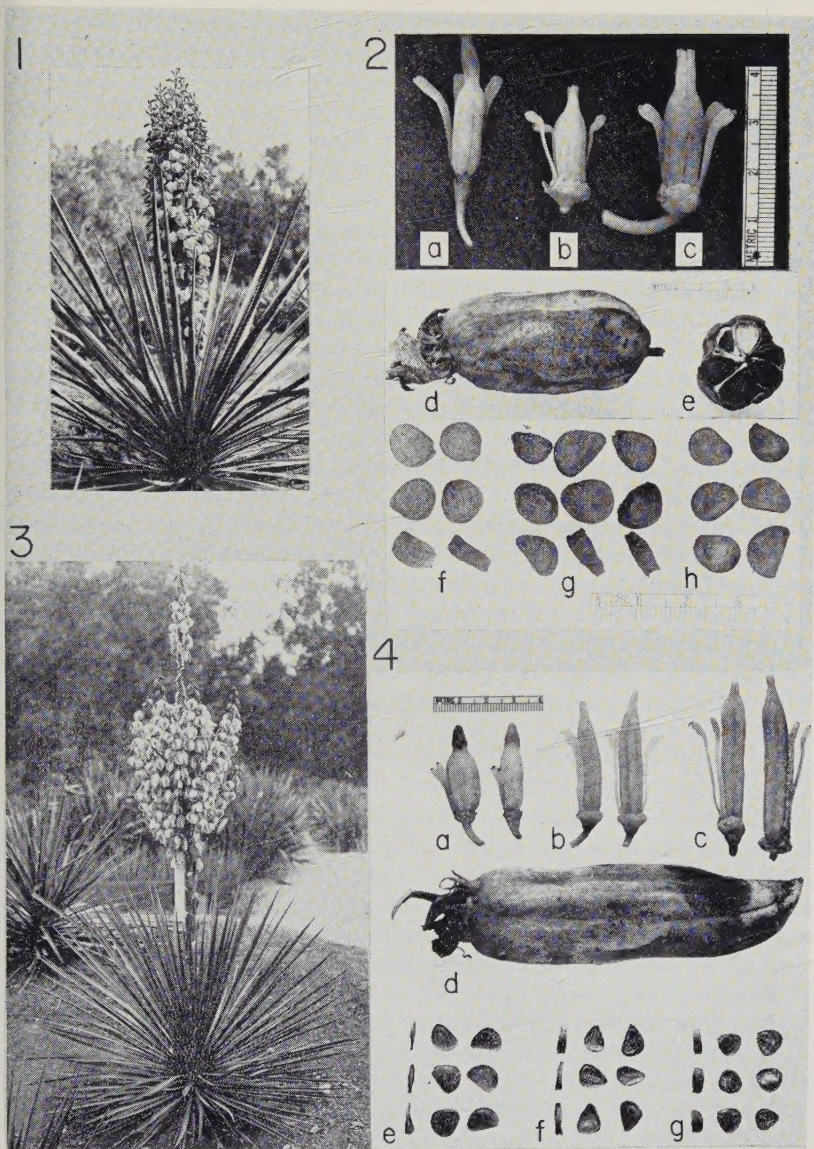
* Fruit percentages based on 25 pollinations and seed germination based on germination test of 50 seeds.

CHARACTERS INDICATIVE OF DERIVATION

The majority of characters of the hybrids are either intermediate in nature or approach those of the parents. The most helpful characteristics in recognizing the derivation of the hybrids are the following:

Yucca glauca \times *Y. elata*: the low height of the inflorescence (7.05 cm. above foliage) and the greenish, swollen styles approximate those of *Y. glauca*, while the large head of leaves and the paniculate inflorescence resemble those of *Y. elata*. The hybrid is very similar to *Y. intermedia* McKelv. var. *ramosa* McKelv. (5,p.120, pl. 46) and to plants reported possibly to be *Y. elata* \times *Y. glauca* hybrids (9, p. 63, pl. 41).

Yucca constricta \times *Y. schidigera* (figs. 1, 2): the non-fleshy fruit (3.20 cm. thick, 6.35 cm. long) and large, angular seeds (7.20 by 11.1 mm.) are characteristic of *Y. constricta*, while the indehiscent fruit and



FIGS. 1-4. *Yucca* parents and hybrids. FIG. 1. Habit of *Yucca constricta* \times *Y. schidigera*. FIG. 2. *Yucca constricta* \times *Y. schidigera* and parents: a, pistil and stamens of *Y. constricta*; b, pistil and stamens of *Y. schidigera*; c, pistil and stamens of hybrid; d, capsule of hybrid; e, cross section of hybrid capsule; f, seeds of *Y. schidigera*; g, seeds of hybrid; h, seeds of *Y. constricta*. FIG. 3. Habit of *Yucca arizonica* \times *Y. neomexicana*. FIG. 4. *Yucca arizonica* \times *Y. glauca* and parents: a, pistil and stamens of *Y. glauca*; b, pistil and stamens of hybrid; c, pistil and stamens of *Y. arizonica*; d, fruit of hybrid; e, seeds of *Y. glauca*; f, seeds of hybrid; g, seeds of *Y. arizonica*.

thick, rough seeds containing ruminate endosperm are characteristic of *Y. schidigera*. The only similar fruits found on native plants (9, p.56, pl.34) occurred on plants belonging to the *Y. glauca* alliance, but these fruits contained typical capsular seeds.

Yucca arizonica \times *Y. neomexicana* (fig. 3) and *Y. arizonica* \times *Y. glauca* (fig. 4) are fairly similar. They differ chiefly in the leaf blades being mainly concavo-convex and the flowers globose in *Y. arizonica* \times *Y. neomexicana*, while the leaf blades are largely plano-convex and the flowers campanulate in *Y. arizonica* \times *Y. glauca*. The most significant features of these hybrids are the following: 1) the non-fleshy, indehiscent fruits and the large, angular, thick, rough seeds containing a ruminate endosperm (fig. 4), which characterize the dehiscent-indehiscent origin of the hybrid; 2) the exceptionally long, conical ovary (3.80 cm.) and fruits (10.3 cm.) (fig. 4), which separate the hybrids from *Y. constricta* \times *Y. schidigera* and possibly characterize all hybrids between species of the *Baccatae* series of McKelv. and dehiscent fruit species; and 3) the paniculate-racemose nature of the inflorescence proper (lower half cuneiform, upper half racemose) (fig. 3), which probably characterizes hybrids between plants with typical paniculate and racemose inflorescences. Although no native plants exhibiting the first two of the preceding features have been reported, those with paniculate-racemose inflorescences are fairly common. Such inflorescences are characteristic of *Y. utahensis* McKelv. and *Y. intermedia*, and they are common among native yuccas reported to be possible hybrids (9, pp.56-68, pl.31, 33, 40).

YUCCA CONSTRICTA \times Y. SCHIDIGERA F₂

Second generation seedlings of only *Y. constricta* \times *Y. schidigera* have been grown. Leaf variations between individuals of a year-old population are as follows: 1.40 cm. wide and 12.0 cm. long to 0.63 cm. wide and 21.3 cm. long; thick, rigid and straight to thin, flexible and falcate; light green to dark green; and thin, entire margin to corneous, denticulate margin. The leaves of several of the seedlings are considerably broader than those of equally as old seedlings of such broadleaved species as *Y. faxoniana* (Trel.) Sarg., *Y. supicola* Scheele, and *Y. gilbertiana* (Trel.) Rydb. Although the seedling leaves of *Y. schidigera* have denticulate margins they become filiferous several months before they are a year old. Corneous, denticulate margins are characteristic of matured leaves in species of the sections of *Hesperoyucca*, *Clistocarpa*, and the series *Rupicola* of McKelv.

DISCUSSION

The normal meiotic behavior and the high fertility of the hybrids indicate that the chromosomes of the parental species are homologous and differ only with respect to certain genes. Furthermore, since the similar karyotypes of yuccas suggest parallel speciation, it is very likely that there is a considerable degree of genetic affinity between the majority of species. Under these conditions it appears that the major barrier to

interbreeding among the native plants of *Yucca* is spatial isolation. Although these suppositions are supported by putative, natural hybrids involving many species, several species are not included. It is very probable, however, that hybrids involving the latter species have not been recognized, or that barriers other than genetic affinity or geographical separation occur.

The fact that no apparent hybrids involving *Y. schottii* Engelm. have been reported is unquestionably due to the late flowering season of this species. Although similar flowering barriers occur between several other species, usually the flowering period within a group of associated species overlaps. The failure of *Y. arizonica* \times *Y. neomexicana* and *Y. arizonica* \times *Y. glauca* to fruit freely was probably due to the long style and closed stigma lobes, which commonly prevented fertilization. It is likely that the capitate stigma of *Y. whipplei* Torr. is a structural barrier and that similar barriers exist in other species.

Although dehiscent- and indehiscent-fruited species are frequently associated, no reputed natural hybrids between them have been reported. In general appearance *Y. constricta* \times *Y. schidigera* resembles an indehiscent, baccate-fruited yucca, while *Y. arizonica* \times *Y. neomexicana* and *Y. arizonica* \times *Y. glauca* resemble a capsular-fruited yucca. If these hybrids were admixed with wild plants, they would undoubtedly be considered hybrids between baccate-fruited species and capsular-fruited species respectively. Their true origin could not be determined without careful examination, unless fruits and seeds were available.

The genera *Yucca* and *Agave* have identical karyotypes (6,10) and a similar distribution (1,8,9), and both are highly unstable (1,7,9). Although much of the diversity in *Agave* is attributed to hybridization, considerable is due to polyploidy, mainly allotetraploidy. The polyploids in *Agave* have a wider distribution and, in general, a greater vegetative development than the diploids (1). No polyploids have been reported in *Yucca*. Both thick, succulent-leaved species (*Y. faxoniana*, *Y. torreyi* Shafer.) and thin, flaccid-leaved species (*Y. constricta*, *Y. glauca*) are diploids (6). Furthermore, the distribution of these diploids is as extensive as the combined diploid-polyploid distribution of *Agave*. *Yucca* extends from south-central Mexico to South Dakota (8,9), whereas *Agave* extends from northern South America to Utah and Nevada (1).

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REVIEW

The Physiology of Forest Trees, a Symposium held at the Harvard Forest, April, 1958, under the auspices of the Maria Moors Cabot Foundation. Edited by KENNETH V. THIMANN with the assistance of WILLIAM B. CRITCHFIELD and MARTIN H. ZIMMERMAN. xvi + 678 pp., illustr. The Ronald Press. New York, N.Y. \$12.00.

Although principles of plant physiology are the same for all forms of plant life, the methods of research will differ depending on what kind of plants are used in experimental work. Truly, it is a great difference in applying plant physiology to cultivated annuals, such as barley or oats on one hand or to forest trees, that may be several hundred years old and many feet tall, on the other. Plant physiologists, working with forest trees have felt for a long time a need for a get-together to discuss their common problems. Dr. Kenneth V. Thimann, Professor of Biology, Harvard University, was responsible for organizing the first International Symposium on The Physiology of Forest Trees. The symposium was held under the auspices of the Maria Moors Cabot Foundation. Over thirty scholars from several European countries, Canada and United States gathered at the Harvard Forest, Petersham, Massachusetts, in April 1957. The topics discussed included: Water relations and sap movement; Photosynthesis; General Biochemistry; Mineral nutrition; Translocation; Root Growth and other phenomena; Photoperiodism and Thermoperiodism; and Reproduction. The papers were edited by Dr. Thimann, with the assistance of Dr. William B. Critchfield and Dr. Martin H. Zimmermann, and published in one volume. Publication of this volume signifies, if not the birth, at least a formal recognition, of a new branch of Plant Physiology.

The import of this book on the further development of Forest Tree Physiology will be felt for a long time.—N. T. MIROV, Pacific Southwest Forest and Range Experiment Station, Berkeley, California.

NOTES AND NEWS

ALPHABETICAL LIST OF FAMILIES FOR MUNZ AND KECK. An alphabetical list of families, giving the page on which each family begins, is available for Munz and Keck, *A California Flora*. It is intended for pasting to the inside of the back cover. Copies may be had by sending a request for the number desired, together with a stamped self-addressed envelope, to Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, California.

Some publications of interest follow:

Origin of Primary Extraxylary Stem Fibers in Dicotyledons, by Amélie Blyth. University of California Publications in Botany 30 (2): 145-232, pls. 1-23. 1958. \$1.75.

Secondary Phloem of Calycanthaceae, by Vernon I. Cheadle and Katherine Esau. University of California Publications in Botany 29 (4): 397-510, pls. 60-67, 109 figs. in text. 1958. \$2.25.

*Ontogeny of the Inflorescence and the Flower in *Drimys winteri* var. *chilensis**, by Shirley Cotter Tucker. University of California Publications in Botany 30 (4): 257-336, pls. 24-33, 43 figs. in text. 1959. \$1.50.